COLLATERAL BUDDING IN ANNELIDS OF THE GENUS TRYPANOSYLLIS.

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ASIDE from the marvelous development of an extensively branching stock in *Syllis ramosa*, the only mode of asexual proliferation hitherto known among annelids is the linear stolonization so well exemplified by species of Autolytus, Myrianida, Procerastea, Nais, and a few other genera of small chætopods. Previous to the discovery of the extraordinary forms about to be described, the production of numerous *collateral* buds from a definite and circumscribed proliferating region has never, it is safe to say, been even imagined as among the possibilities of annelid development.

As briefly announced more than a year ago,[1] two species of Syllidæ living on our Pacific coast have been found to produce sexual zooids by collateral budding. These I have studied as fully as the scanty material permits, and the results, though far from complete, are, I trust, of sufficient interest to warrant their publication, particularly as the obtaining of more material is a matter of great uncertainty.

Both species undoubtedly belong to the genus Trypanosyllis as defined by Malaquin,[2] and both are unusually large for syllidians. The larger, for which the name *Trypanosyllis ingens* is proposed, is a veritable giant of its kind, measuring 13 cm. in length, exclusive of the tail buds, and 6 mm. in width. The only specimen of this rare species I have seen was given to me by Prof. Harold Heath of Stanford University, to whom my grateful acknowledgments are due. It was found by him under a stone between tide marks, at Pacific Grove, California.

[1] Johnson, H. P. A New Type of Budding in Annelids. Paper read at the eleventh annual meeting of the American Morphological Society at Baltimore, Dec. 27, 1900. An abstract was published in the *Biological Bulletin*, vol. ii, No. 6 (1901). [2] Malaquin, A. *Recherches sur les Syllidiens*, p. 72. Lille, 1893.

The worm is much flattened in the horizontal plane, measuring only 2 mm. in its greatest dorso-ventral diameter. The parapodia (Fig. 1) are very diminutive for the size of the trunk, and the somites are so short that the stout dorsal cirri (inasmuch as their thickness exceeds the length of the somites) form an alternating series. The somites number nearly 500.

As *Trypanosyllis ingens* is undoubtedly new to science, a diagnostic description, with figures sufficient for its identification, is given. It is unfortunately too rare to serve as a

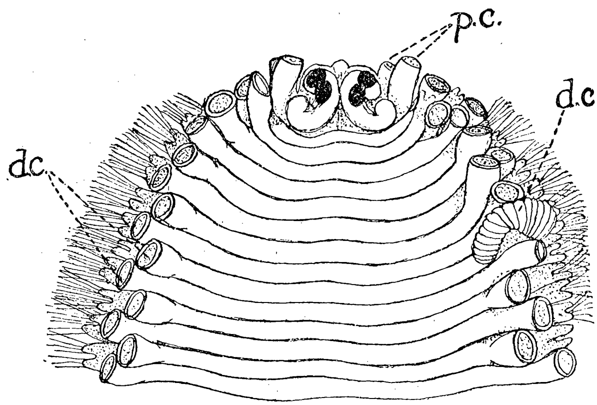

FIG. 1. — Anterior extremity of *Trypanosyllis ingens.* The palpi, antennæ, median cirrus, peristomial cirri, and all the dorsal cirri, with one exception, are broken off at the basal constriction. *p.c.*, peristomial cirri; *d.c.*, dorsal cirri. × 12.

subject for study of collateral budding. It occurs in none of the numerous gatherings of Pacific coast Polychæta that came into my hands during six years' residence in California; and Dr. Heath, who has done a great deal of collecting at Pacific Grove and vicinity at all seasons of the year, informs me that he has found only this specimen.

Trypanosyllis ingens sp. nov.

Form elongated, broad, much depressed; dorso-ventral differentiation very slight, dorsum slightly convex, ventral surface plane, longitudinally bisected by a narrow median welt, sharply bounded by two fine parallel grooves; extremities evenly and abruptly rounded off; slightly more tapered posteriorly than anteriorly; somites very short, crowded, about 476 in number.

General coloration tawny; parapodia, dorsal cirri, and anterior extremity, purple; caudal buds, from presence of ova, rich yellow.

Prostomium (Fig. 1) trapezoidal, its length two-thirds of its width, distinctly bilobed, the lobes scroll-shaped, with a deep median notch at posterior border; eyes 4, on anterior scrolls, connate. Palpi, antennæ, and median cirrus, all wanting in the type specimen.

Peristomium somewhat broader than the prostomium, enclosing the latter posteriorly and on the sides; with dorsal and ventral peristomial cirri (Fig. 1, *p.c.*).

Parapodia uniramous, short, crowded, with bases of the dorsal cirri interlocking (Fig. 1, *d.c.*); dorsal cirri (Fig. 2, *d.c.*) thick, coiled, articulated, rather rapidly tapering towards the tip; ventral cirrus tongue-shaped or fusiform; setæ (Fig. 3) 11–13 in each foot, with

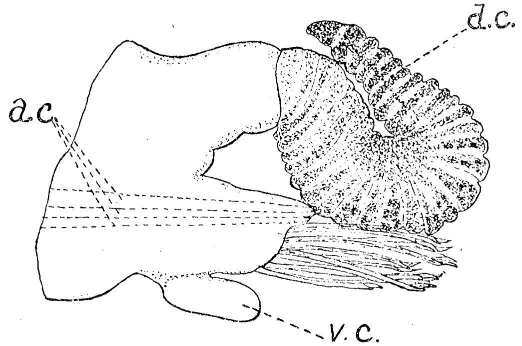

Fig. 2.

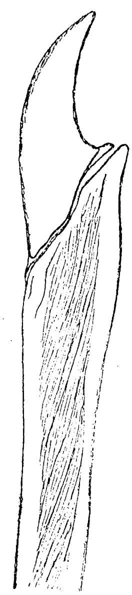

Fig. 3.

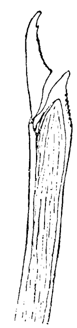

Fig. 4.

Fig. 2.— Foot of *Trypanosyllis ingens*, from about the middle of the length. *ac.*, aciculæ (three); *d.c.*, dorsal cirrus; *v.c.*, ventral cirrus. × 30.
Fig. 3.— Seta of the same, in profile. × 467. Fig. 4.— Seta, sexual zooid of the same. × 467.

toothless hooked appendage; aciculæ (Fig. 2, *ac.*) 3–5, their distal ends extending into two finger-like lobes, one usually much thicker than the other, at the dorsal tip of the foot.

Mouth large, its transverse diameter equal to width of prostomium; bounded by 7 crenulations. Somites 1–8 curved backward around mouth, as in Amphinomidæ and Palmyridæ.

Proboscis short and small (2 mm. long), thin-walled, bounded posteriorly by a double ring of fleshy papillæ, 9–10 in each ring, those of the outer circle more than twice as long as the inner ones.

Œsophagus short (3.5 mm.), and of small diameter (1 mm.) for the size of the animal, with usual chitinized lining, which terminates in a "trephine" anteriorly. Œsophagus surrounded

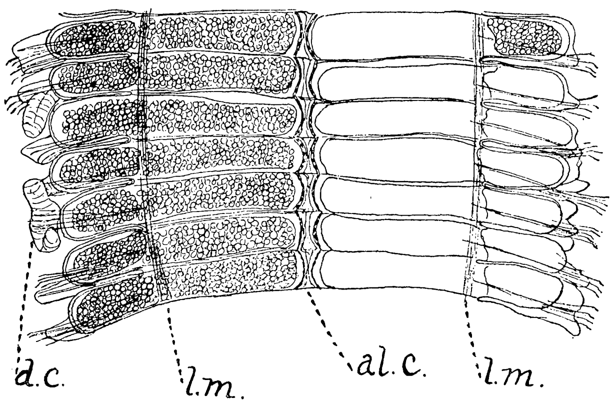

FIG. 5. — Seven somites from the middle region of a female sexual zooid of *Trypanosyllis ingens*, viewed from the dorsal aspect. With two exceptions (*d.c.*) the dorsal cirri are broken off. The rudimentary alimentary canal (*al.c.*) is indicated; also the ova on the left side and in one parapod on the right. The longitudinal muscle bands (*l.m.*) mark the bases of the parapodia. In clove oil. × 19.

by 9–10 glands, of wavy or crenulate outline, opening near the papillæ, their blind ends extending back a short distance on the proventriculus.

Proventriculus also small for size of the animal, 6 mm. long, 1.5 mm. in greatest transverse diameter, slightly club shaped, thickest anteriorly, tapering gradually to posterior end; two well-defined raphes. No cœca were detected.

Intestine with extensive paired diverticula in every somite back of the proventriculus.

Sexes distinct; sexual products, so far as known, developed only in a cluster of collateral buds, growing from a definite proliferating region near the posterior end; probably also in the parental somites posterior to the budding zone.

Length, 130 mm.; greatest transverse diameter, including parapodia, 6 mm.; dorso-ventral diameter, 2 mm.

Habitat, Pacific Grove, California; between tide marks.

The form seemingly most nearly allied to *T. ingens* is *Trypanosyllis gigantea* (M'Intosh) Ehlers of the Southern Ocean. The latter is but little inferior in size, measuring, according to M'Intosh,[1] 90 mm. in length and 7 mm. in breadth. The form

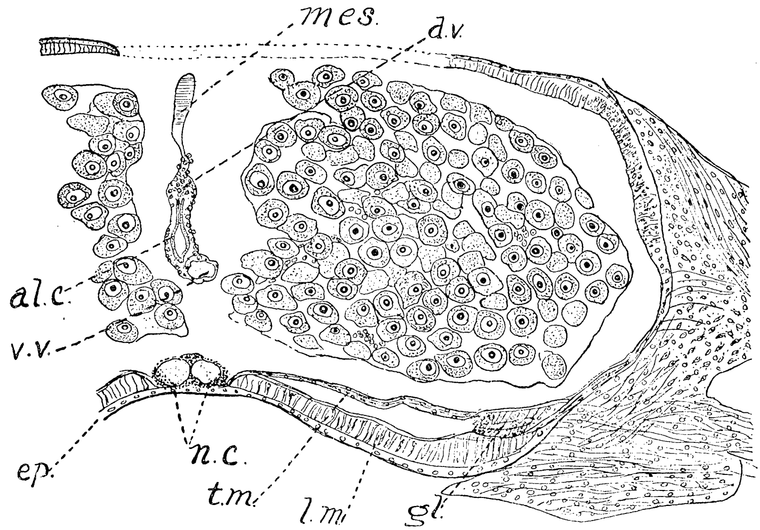

FIG. 6.—Transverse section, female zooid of *T. ingens*, right half. A portion of the dorsal body wall (indicated by dotted lines) is broken away. The plane of the section encounters the septum on the right. *al.c.*, rudimentary alimentary canal; *d.v.*, dorsal blood vessel; *v.v.*, ventral ditto; *mes.*, dorsal mesentery; *gl.*, problematic glandular structure (external extremity); *n.c.*, nerve cords; *l.m.*, longitudinal musculature; *t.m.*, transverse muscle; *ep.*, epidermis. × 100.

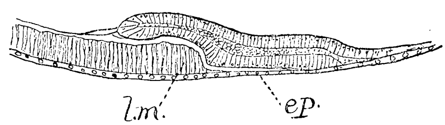

FIG. 6 *A*.—Problematic gland-like tube, from right side of another section of the same series, with portion of body wall adjacent. The external extremity (aperture?) is toward the right. The tube is laid open by the section, showing ends of columnar cells. Lettering as in Fig. 6. × 100.

is very similar, the parapodia of both have multiple aciculæ (6 in *T. gigantea*), and the setæ of the two species are practically identical. There is nothing, however, in M'Intosh's description or in his figure of a cross-section to indicate that

[1] M'Intosh, W. C. Challenger Reports. *The Polychæta*, vol. xii (1887), p. 193.

T. gigantea has the great intestinal diverticula so conspicuous in *T. ingens* and in *T. gemmipara* (Fig. 16). The prostomium of *T. gigantea* is also of simpler form.

Unfortunately the delicate tail buds of this formalin-preserved specimen were somewhat macerated and broken in transportation ; most of them had fallen off, and probably some of them were missing, when the specimen came into my hands. They number about 30, and are all at about the same advanced stage of development. Each bud exhibits the external characters of the stock. Its somites have nearly the same proportions ; its parapodia, with their diminutive cirri and setæ (Fig. 5), are of the same pattern, with the slight difference that the appendages of the setæ have a small tooth and minute serrations on the concave side, while these are absent in the setæ of the stock (*cf.* Figs. 3, 4). The average length of the buds is 5 mm., their breadth 2 mm., their thickness 0.5 mm. The number of their somites is approximately 25.

Each zooid is divided into a double series of cœlomic spaces by the intersegmental dissepiments and a minute median tubular structure, which I interpret as a rudiment of the alimentary canal (Figs. 5, 6, *al.c.*). The cœlomic spaces, including even the parapodial cavities (Fig. 5), are packed full of eggs, which possess very large nuclei and nucleoli, the latter usually vacuolated (Fig. 6). No ova have been found in the parent stock. The longitudinal muscular system of the bud is not highly developed (Figs. 5, 6, *l.m.*), and no circular musculature was detected. Circular muscles are very slightly developed in the stock. There is a slender transverse muscle extending from the lateral body wall to the nerve cord (Fig. 6, *t.m.*). This, however, I suspect is not so much a separate muscle as a portion of the very extensive system of septal muscles.

A dorsal and a ventral blood vessel (Fig. 6, *d.v.*, *v.v.*) are seen close to the digestive tract. The ventral vessel with its coagulum is apparently of uniform diameter throughout its course, while the dorsal vessel is segmentally constricted (Fig. 6 represents a constricted place). No lateral branches have been detected.

A pair of problematic organs, possibly much-modified nephridia, are present in each segment. These organs are tubular, with rather narrow lumen, their thick walls composed of columnar, much-vacuolated cells (Fig. 6 *A*), and no opening has been seen at either extremity. They occupy a ventral position, the internal extremity being directed towards the median line, and the outer extremity obliquely towards the

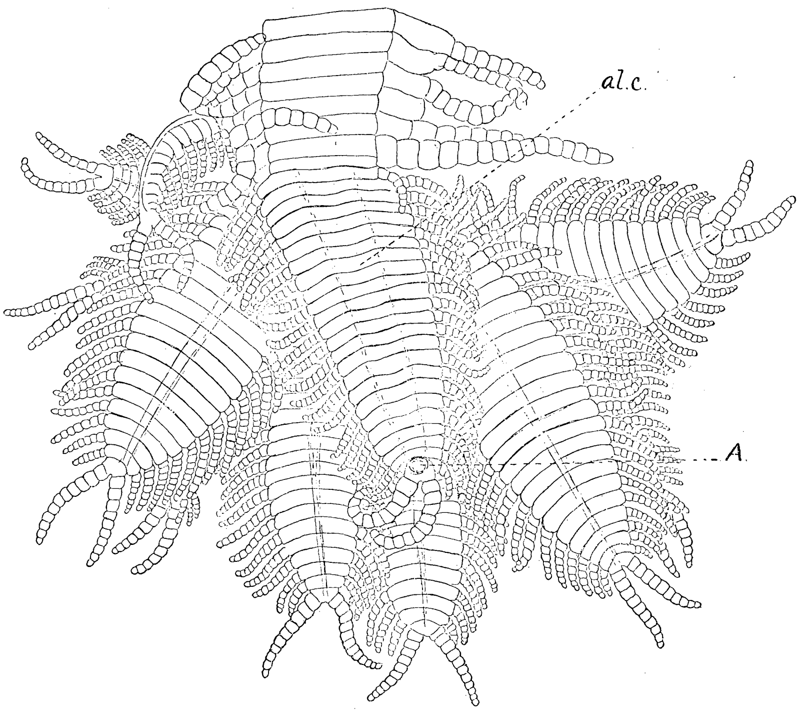

FIG. 7.—Caudal buds of *Trypanosyllis gemmipara*, dorsal aspect. The posterior ciliated portion of the intestine (*al.c.*) and the anus (*A*) are shown in the attenuated caudal portion of the stock. × 26.

ventral body wall, which it penetrates as far as the epidermis. It is known that in several species of syllidians the segmental organs serve as genital ducts, and for this purpose undergo enlargement at sexual maturity.[1] Such a function would seem to be impossible in this instance when we compare the diameter of the ova with the diameter of the tubes.

[1] Ehlers, Ernst. *Die Borstenwürmer* (1864), p. 215.

A pair of ventral nerve cords (Fig. 6, *n.c.*) are conspicuous in transverse sections, in which the cut ends of the nerve fibers appear, surrounded at intervals by a few darkly stained bodies, the nuclei of ganglionic cells. The ganglia, one to each segment, can be plainly seen in a zooid cleared with glycerine. The nerve cords, although in direct contact with the epidermis, are plainly not fused with it.

No head or eyes were detected; but as these structures are obviously present in the zooids of the closely allied *Trypanosyllis gemmipara*, failure to find them in the present species is almost certainly due to the broken condition of the material, the tips of the buds being especially liable to injury.

The place of origin of the buds is near the posterior extremity of the stock. Probably, as in *T. gemmipara*, it is about the length of a zooid, or twenty somites, in front of the pygidium. The proliferating region, although now destitute of buds, has been sectioned, and shows merely a mass of undifferentiated tissue pervaded by a radiating system of muscle fibers, which, in all probability, passed into the zooids, as they certainly do in *T. gemmipara.*

The rudimentary and apparently functionless condition of the alimentary canal is noteworthy. Although impossible, from the defective material, to tell whether a mouth and anus are really absent, it is highly probable that they are.

Trypanosyllis gemmipara.

The other species with collateral buds was found in a collection of Polychæta gathered in Puget Sound and vicinity by Nathan R. Harrington, since deceased, member of the expedition sent out by Columbia University in the summer of 1896. It has been described and figured in the writer's report[1] on the Polychæta of that expedition under the name *Trypanosyllis gemmipara*.

Although much smaller than the preceding, *T. gemmipara* is nevertheless very large for a syllid. The Puget Sound specimen measures 68 mm. in length and 3 mm. in width. Like

[1] Johnson, H. P. The Polychæta of the Puget Sound Region, *Proc. Boston Soc. Nat. Hist.*, vol. xxix (1901), No. 18, p. 405, Figs. 72–76.

T. ingens, and in fact most, if not all, species of this genus, *T. gemmipara* is much flattened horizontally, being only 1 mm. in dorso-ventral diameter. The somites number about 300, and, as in *T. ingens*, their width many times exceeds their length.

The tail buds, 50 in number, present all stages of development. They form a tuft arising from the ventral aspect near the posterior extremity, and superficially resemble a bunch of

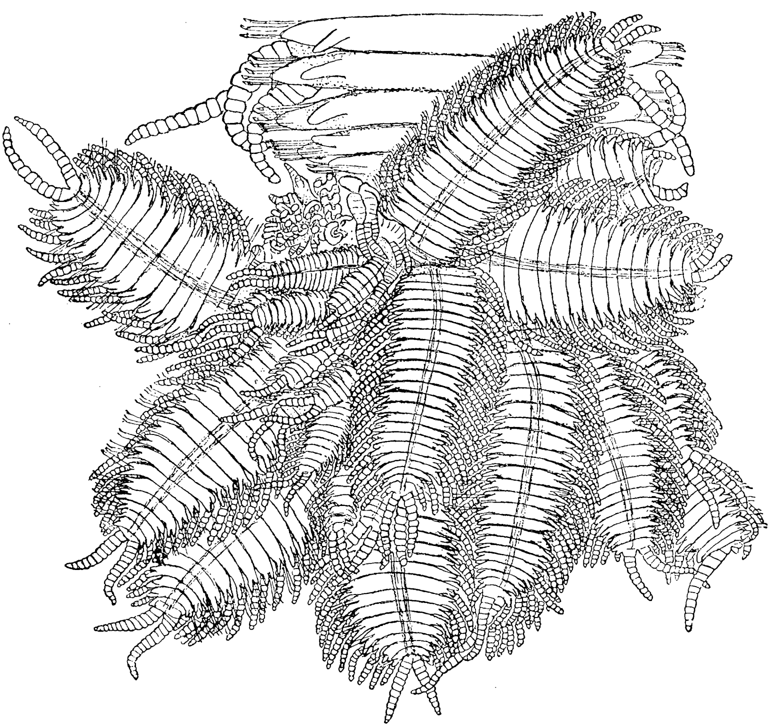

FIG. 8.—Caudal buds, ventral aspect, of *T. gemmipara*. The young buds are seen on the left of the figure. × 26.

ferns (Figs. 7, 8). Neither as regards position nor order of development do they obey the laws of bilateral symmetry. The whole cluster is bent to the right, making an angle of about 25° with the longitudinal axis of the worm. Only 13 of the buds have reached an advanced stage of development; these are elliptical in shape, rather thin in proportion to their other dimensions, and possess the chief external characters of

the parent. Their somites are 20 to 28 in number; their small but well-developed parapodia are furnished with moniliform dorsal cirri and minute setæ of the same form as those of the parent. The average length of a mature bud is 2.5 mm.;

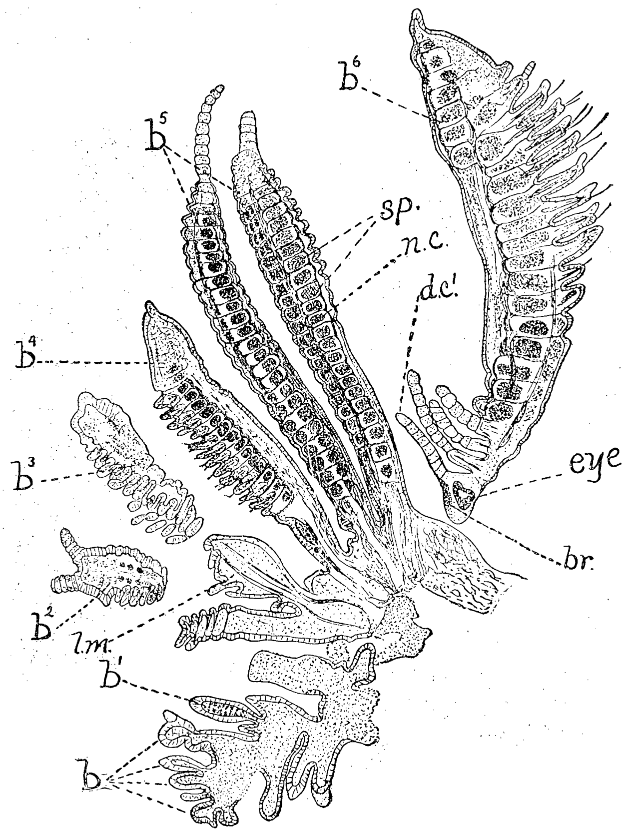

FIG. 9.—Frontal section through budding zone of *T. gemmipara*, showing male zooids at different stages (b–b^6) of development. The zooids are cut at various planes (the two in the center of the figure, marked b^5, nearly in the median sagittal plane). The youngest buds are marked b; b^1 indicates a bud in which segmentation is just beginning; b^2, b^3, buds in which segmentation is completed except at distal end, and the parapodia are already well developed; b^4–b^6, buds progressively older; *br.*, brain; *d.c.*^{1}, first dorsal cirrus; *l.m.*, longitudinal muscles; *n.c.*, nerve cord; *sp.*, sperm cells. × 50.

the breadth, including parapodia, is 1 mm. The bud tapers more towards the caudal than towards the cephalic extremity. The anal cirri are longer and thicker than any of the dorsal cirri (Figs. 7, 8).

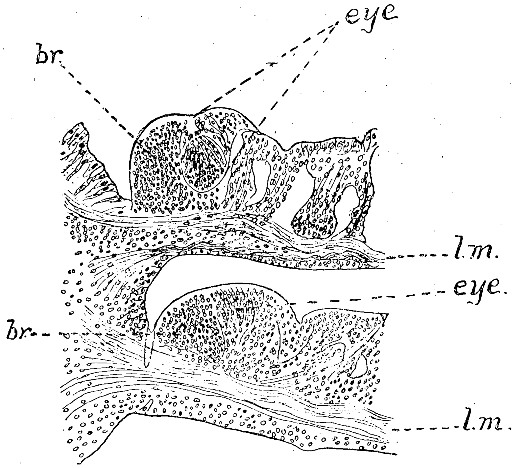

FIG. 9 *A*. — Anterior extremities of zoOids marked b^5 in Fig. 9, showing, at two different stages, the *Anlagen* of eye and brain as they appear in a section further from the median plane of the zooids than that represented in Fig. 9. The extension of the ventral longitudinal muscles of the zooids into the proliferating zone of the stock is clearly indicated. Lettering as in Fig. 9. × 200.

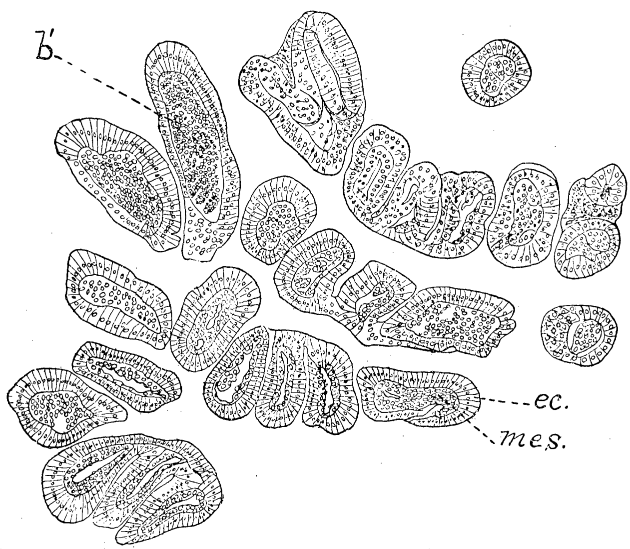

FIG. 9 *B*. — Transverse section of group of young buds, taken in same direction (frontal), but at lower level than Fig. 9. The arrangement in transverse rows is clearly indicated. Buds at extreme left are cut obliquely; in one of these (b^1), segmentation of the mesoderm is beginning. *ec.*, ectoderm; *mes.*, mesoderm. (Semidiagrammatic.) × 147.

Only advanced buds are visible from the dorsal aspect (Fig. 7). These completely cover the young buds on the ventral side and overlap so that the heads of all the advanced buds are concealed. Occupying the most dorsal position amongst the advanced buds is the attenuated and rapidly diminishing caudal extremity of the stock. It is much like the buds in general aspect, and further resembles them in containing sperm cells, which are absent in all portions of the stock in front of the proliferating region. It differs from the buds in possessing (1) a heavily ciliated continuation of the alimentary canal (Fig. 7, *al.c.*), (2) the anus, and (3) differs in lacking cephalization. In every respect except that it contains sperm cells, it resembles a regenerated posterior extremity. It possesses twenty-four somites, including the pygidium. The proliferating region is therefore this number of somites in front of the posterior extremity. As Fig. 7 shows, the attenuated posterior portion has almost as much the appearance of being an appendage to the budding zone as any of the mature buds.[1]

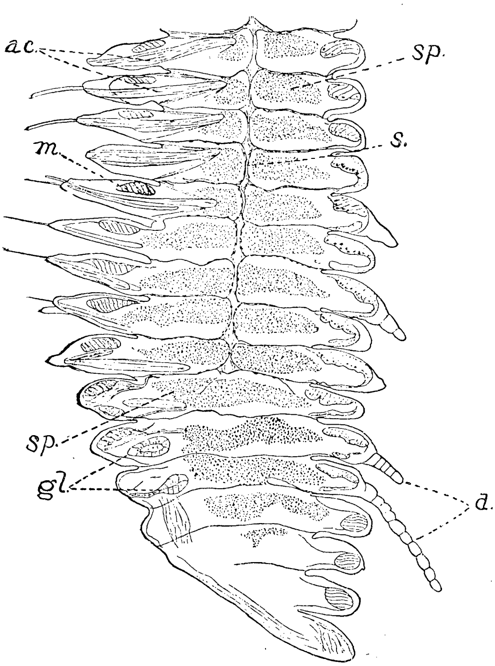

FIG. 10. — Frontal section of a portion of a full-grown bud of *T. gemmipara*, showing sperm masses (*sp.*), parapodia, dorsal cirri (*d.c.*), setæ, aciculæ (*ac.*), muscles (*m.*), and parapodial glands (*gl.*). The intersegmental dissepiments and median strand (*s.*) are indicated. × 75.

It is worthy of note that into this region the deep intestinal

[1] This attenuated posterior extremity is probably a permanent feature. I have found it in every entire specimen of *T. gemmipara* I have collected on the California coast, but the number collected is small.

diverticula do not continue. The diverticula of this portion of the alimentary canal are very shallow, and were not detected in the entire specimen (Fig. 7).

The attachment of the buds to the proliferating area (invisible in the entire specimen) is by a short unsegmented pedicle at the cephalic extremity of each bud (Figs. 9, 9 *A*, 17, *p.*). There is no distinct prostomium. The head is merely the eye- and brain-bearing first segment, which shows its primitive character by also carrying parapodia equipped with dorsal cirrus, setæ, and aciculæ (Fig. 9, *d.c.'*). This fact is significant, because it is exactly what we find in the stolons of not a few syllidians, among others those of *Trypanosyllis krohni*.[1]

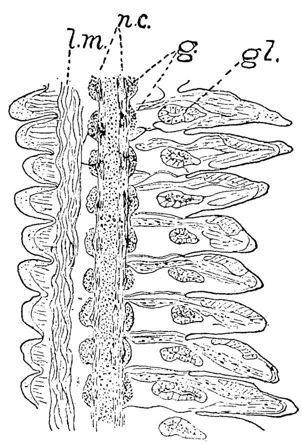

FIG. 11.— Frontal section at a lower level, showing paired nerve cords (*n.c.*), ganglia (*g.*), ventral longitudinal muscle (*l.m.*), and parapodial glands (*gl.*). × 75.

The eyes, apparently only two (although each may represent two, completely fused), are large and highly developed, as is often the case in stolons. There is a well-defined lens (Fig. 15, *l.*), a "vitreous body" (*vt.*) composed of the rods of the retinal cells, and a very thick, cup-shaped retina, the inner layer of which contains a small quantity of brown pigment (*p.*), but not dense enough to conceal its structure.

The buds are destitute of an alimentary canal, unless the merest rudiment exists in the form of a median strand (Figs. 10, 12, *s.*). Certainly there is no tubular structure such as occurs in the bud of *T. ingens*. There is no mouth, anus, or blood vessels. The zooid is sharply divided by the dissepiments and an incomplete median partition into a double series of cœlomic spaces. That the right-and-left cœlomic chambers of the same somite are sometimes continuous is clearly shown by the sperm masses in the more posterior segments represented in Fig. 10. This seems to be the case only in the ventral portion of the chamber. The sperm masses do not

[1] See Malaquin, *op. cit.*, Pl. X, Figs. 18, 19.

completely fill the spaces, and do not seem in any case to occupy the cavities of the parapodia. Spermatozoa were not observed in any of the buds, indicating that even the oldest are not fully ripe.

The parapodia are fully equipped with dorsal and ventral cirri, setæ, a pair of aciculæ, — the latter projecting deeply into the sperm masses (Fig. 10, *ac.*), — and the usual musculature. Occupying a large portion of the cavity of each parapodium are pouch-shaped glandular structures of unknown function. Each is composed of a few very large vesicular cells, and has a good-sized lumen which appears to open near the base of the parapodium, on the ventral side (Figs. 10, 11, 13, *gl.*). No actual opening, however, has been found, and the mouth seems entirely blocked by columnar epidermal cells (Fig. 13). These glands occur in the segments of the attenuated caudal region, where they have the same size and aspect as in the buds. In the parapodia of the stock — at least those immediately in front of the budding zone — they are also found. Without much doubt these structures are homologous with the parapodial glands (*glandes pédieuses*) known to be present in *Trypanosyllis cœliaca* and in species of other genera of Syllidæ.[1] Their function is the secretion of mucus. From their histological aspect, this is probably likewise the function of the above-described glands.[2]

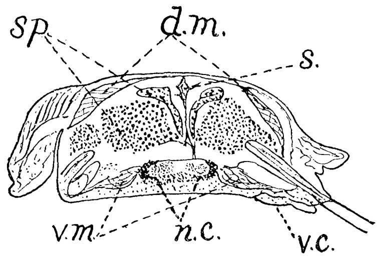

FIG. 12.—Transverse section of full-grown bud, *T. gemmipara*. *d.m.*, dorsal longitudinal muscles; *v.m.*, ventral ditto; *s.*, median strand; *v.c.*, ventral cirrus; *sp.*, masses of sperm cells; *n.c.*, ventral nerve cord, showing cut ends of fibers and ganglionic cells. × 100.

There are two large and conspicuous ventral nerve cords, with paired ganglia in every somite (Figs. 11, 12, *n.c.*, *g.*). Proportionately to the size of the bud, the nervous system is much larger in this species than in *T. ingens*. As accurately as could be made out from the single series of sections, the

[1] See Malaquin, *Recherches sur les Syllidiens*, p. 87, Pl. VII, Fig. 7.

[2] It is interesting to find that these glands are not only relatively, but absolutely, larger in the caudal segments and in the buds than in the stock.

nerve cords run forward to the cephalized extremity and there innervate the eyes and a darkly staining mass of ectodermic cells which probably functions as brain (Fig. 14, *cb.*). Although the nerve cords are plainly separate from the epidermis, as shown by a cross-section (Fig. 12, *n.c.*), the brain is no more than a thickened portion of the epidermis, and fully confluent with it. As clearly shown in one section (Fig. 14), the optic nerve comes from the ventral cord, and not from the brain.

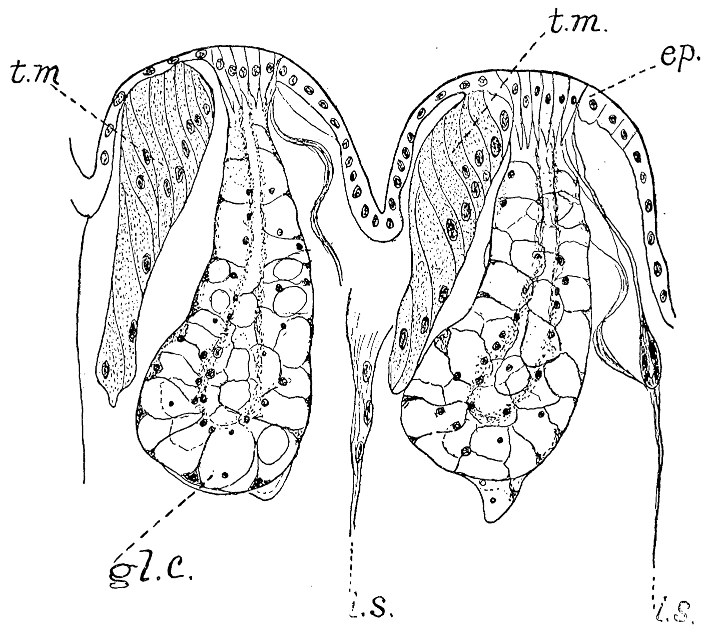

FIG. 13. — Two pedal (mucous?) glands of bud of *T. gemmipara*, in longitudinal section. The lumens of the glands are bounded by stippled bands; the gland cells (*gl.c.*) are highly vacuolated; the epidermal cells at mouth of glands are columnar. *t.m.*, transversal muscles; *i.s.*, intersegmental dissepiments; *ep.*, epidermis. × 525.

When viewed from the ventral aspect the cluster of buds presents an interesting condition of things (Fig. 8). On the right, at the base of the cluster, is a group containing about 25 very young buds (Fig. 8), as yet showing no segmentation, but each with two distal processes which are the *Anlagen* of the anal cirri. As may clearly be seen in a transverse section of the group (Fig. 9 *B*), the buds are arranged in rows, partly transverse and partly longitudinal as regards

the long axis of the stock. In a graduated series proceeding from the left side of the cluster of youngest buds are more advanced buds, the largest approaching the mature condition (Fig. 9, *b*–*b*⁶). At an early stage the anal cirri attain a notable length and become articulated.

As shown in a frontal section (Fig. 9) through the proliferating region, the buds sprout from a mass of undifferentiated tissue traversed by muscle fibers which are continuous

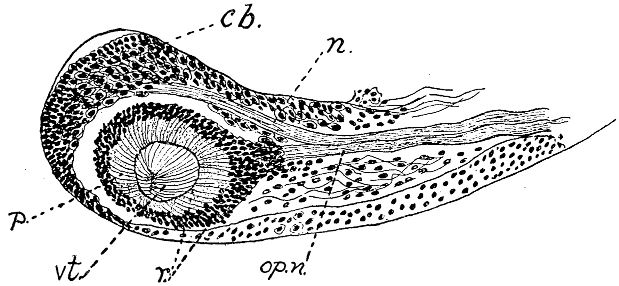

FIG. 14. — Frontal section of a portion of head, same bud as shown in Fig. 10. *n.*, nerve to brain (*cb.*); *op.n.*, optic nerve; *r.*, retina, showing rod cells and pigment (*p.*); *vt.*, "vitreous body," composed of the clear retinal rods. The nerve to the brain breaks up into numerous fibers, which are distributed to the ganglionic (?) cells. × 153.

with the longitudinal muscle bands of the buds (Fig. 9 *A*, *l.m.*). This mass is mesoderm, covered by ectoderm in the form of epidermis. Both ectoderm and mesoderm of the buds are continuous with the same germ layers of the proliferating region. Whether the proliferating mass comprises one or more than one somite cannot be positively stated from the sections at hand, which are defective at this point.

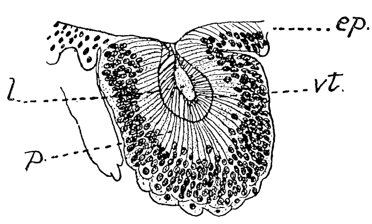

FIG. 15. — Longitudinal section of eye, showing its cup-like form, and apparent formation by an invagination of the epidermis (*ep.*). Lettering as in preceding figure; *l.*, lens. × 267.

At a very early stage the mesoderm undergoes segmentation, and the reproductive cells are discernible (Figs. 9, 9 *B*, *b'*).

No buds provided with special natatory setæ (*Pubertätsborsten*) such as usually occur in the stolons of syllids and in the sexual buds of *Syllis ramosa*[1] were observed.

[1] M'Intosh. *Challenger Reports*, vol. xii, p. 201, Pl. XXXIV A, Fig. 9.

General Considerations.

From the standpoint of comparative morphology, the collateral buds of Trypanosyllis may be regarded as structures of the same order as the stolons of Autolytus or Myrianida, but with the important difference that the buds in this case are lateral outgrowths, whereas in stolonization they are the result of linear growth and differentiation. As stolons, they extend the organic axis of the parent, and the alimentary canal passes through them all, to terminate at the anus located in the pygidium of the oldest stolon.

At first thought it would seem as though the buds of Trypanosyllis are more appropriately comparable to the sexual zooids of *Syllis ramosa*. The superficial resemblance to the latter is indeed striking. In both instances we have a lateral outgrowth of the stock, to which it is attached at the head end by a pedicle; in both, the zooids are the bearers of the sexual products (which do not develop in the stock), and both have an imperfectly developed prostomium bearing highly developed eyes. There are, however, two important points of difference: (1) the pedicle of the sexual zooid of *Syllis ramosa* is segmented, and the segments even bear rudimentary cirri [1]; (2) the sexual zooids as well as the asexual branches of *S. ramosa* contain a branch of the alimentary canal, fully continuous with that of the stock. In neither of these respects does the sexual bud of *T. gemmipara* in the least resemble the sexual bud of *S. ramosa*. The sexual zooids of the latter species are evidently specialized, fructifying branches of a widely branching asexual stock. They are equipped with large eyes and special swimming organs (natatory setæ), and break away from the parent stock at maturity. In all these respects they differ, it is true, from the purely vegetative branches, but these differences are merely adaptive to the special functions of insuring fertilization of the eggs and disseminating the species.

Whether the somite or somites from which the sexual buds of Trypanosyllis arise is to be regarded as homologous with the others cannot be decided from the material at hand. No

[1] M'Intosh. *Challenger Reports*, vol. xii (1887), Pl. XXXIII, Fig. 11.

somite unprovided with parapodia of the usual form was discovered. A recent study of *S. ramosa* by Oka[1] has brought out the interesting fact that the paired buds arise, not from one of the original somites, but from a newly developed, intercalated somite, which differs from all the others in lacking parapodia. Oka is doubtless right in regarding it as non-homologous with the other somites.

While the stolons of Autolytus and of syllidians generally are distinct and complete individuals provided not only with

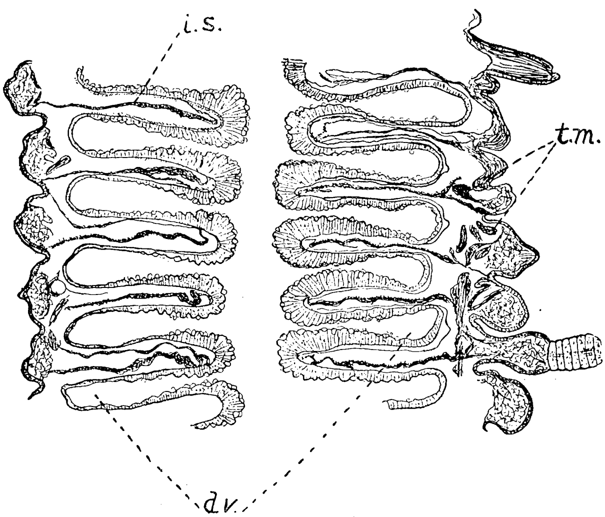

FIG. 16. — Frontal section of stock, *T. gemmipara*, showing the paired intestinal diverticula. The intestinal epithelium gradually thins towards the blind extremities of the diverticula. The intersegmental septa (*i.s.*) and some of the transversal muscles (*t.m.*) are shown. × 34.

sexual, sensory, and locomotor organs, but with those subserving nutrition, circulation, and excretion, the sexual buds of *T. ingens*, and even more strikingly *T. gemmipara*, exhibit a higher degree of specialization in lacking functionally developed vegetative organs. The zooid is therefore quite as incapable of leading a prolonged independent existence as the famed Palolo of the South Seas. It is no more than a living engine for the dissemination of the genital products which it carries,

[1] Oka, Asajiro. Ueber die Knospungsweise bei Syllis ramosa, *Zoölogical Magazine*, Tokyo, vol. vii (1895), p. 117.

and that duty must be accomplished solely by the expenditure of the stored-up energy which it has derived from the stock.

From the biological point of view the function of the zooids is the same, whether they arise by linear or by collateral budding. In both cases there is an alternation of generations exactly comparable to that of the Hydromedusæ. As regards *S. ramosa* the asexual stock is practically as sessile as the sponge in which it lives, and like sessile organisms of much lower grade it branches with great freedom and facility. It is not in the least surprising, therefore, to find such a form producing by lateral budding free-swimming zooids, which serve as special disseminators of the species and provide for a sexual reproduction in which cross-fertilization is assured.

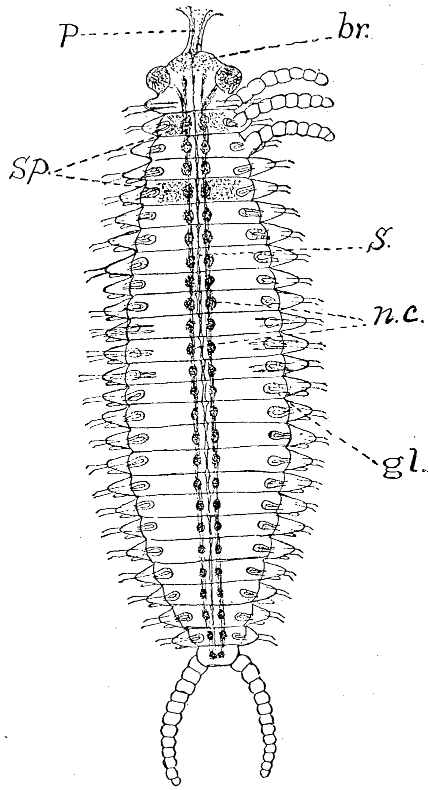

Fig. 17. — Ideal reconstruction of a mature male zooid of *T. gemmipara*. The dorsal cirri are omitted except on right side of three most anterior somites. The sperm masses are in every segment except the first and the pygidium, but are represented only in somites 2 and 5. The aciculæ are omitted except in first segment and three middle ones. *p.*, pedicle of attachment. Other lettering as in preceding figures.

In the forms under consideration the case is somewhat different. Notwithstanding their large size and heavy form, so different from the majority of syllidians, suggest that they are somewhat sluggish in their habits, neither of them can be considered as sessile. It is difficult to see, however, that they are any more inert than a multitude of annelids which have nothing aberrant in their mode of reproduction. Evidently some more precise explanation must be sought.

The fact that Trypanosyllis is a genus of the Syllidæ must not be overlooked. Of all the annelids, this family affords the best and most numerous examples of asexual reproduction by stolonization. The small size and comparatively simple structure of most syllidians no doubt peculiarly adapt them to this mode of multiplication. On account of its great advantage in the dissemination of the species, this form of reproduction, acquired by the presumably diminutive ancestors of the two gigantic species of Trypanosyllis, might be retained in a gradually modified form as by slow degrees the animal became larger and more complex. By equally slow degrees the collateral type of budding would replace the linear.[1] The development in both collaterally budding species of extensive intestinal diverticula (Fig. 16) in every somite from the proventriculus to the budding zone would obviously render inconvenient, if not impossible, the production of large gonads in the stock. As in many other syllidians the production of sexual cells would be more and more relegated to the most posterior somites, and to any linear or collateral buds that might develop in that region.

The advantages of collateral over linear budding in greater safety and compactness, as well as the possibility of securing a more rapid development and a greater number of buds, are obvious. Species of Myrianida produce stolons with the greatest number of zooids, but the chain is not known to have over thirty zooids at any one time.[2] This is only 60 per cent of the number of collateral buds present in the specimen of *Trypanosyllis gemmipara* that has been studied. The 50 buds of the latter add practically nothing to its length, while the 29 buds of the example of Myrianida figured by Malaquin form a chain no less than 55 per cent of the entire length of the worm. The liability to loss or injury to which such a

[1] In *T. zebra*, according to an observation recorded by Viguier in 1886 (*Arch. de Zool. Exp.*, sèr. 2, tome iv, p. 364, footnote), to which the author has kindly drawn my attention, there occurs an apparently non-terminal stolonization which perhaps is a step towards collateral budding. It is not well, however, to push the comparison very far, as there is really little likeness between the two types of gemmation as we know them at present.

[2] See Malaquin, *loc. cit.*, Pl. I.

lengthy chain would be exposed, particularly if very slender and attached to a stock of vastly greater bulk and strength, is evident.

The absence of organs of nutrition, the collateral mode of origin, and the fact that the smaller and simpler members of the genus still produce stolons point unmistakably to the high degree of specialization attained by the sexual zooids of these two species of Trypanosyllis. Both in their structure and in their mode of development they unquestionably represent the most specialized mode of asexual reproduction, not only among the Syllidæ, but among all known annelids.